Common Marmoset (Callithrix jacchus) Personality

Koski, Sonja E.

2017-11

Koski , S E , Buchanan-Smith , H M , Ash , H , Burkart , J M , Bugnyar , T & Weiss , A 2017 , ' Common Marmoset (Callithrix jacchus) Personality ' , Journal of Comparative Psychology , vol. 131 , no. 4 , pp. 326-336 . https://doi.org/10.1037/com0000089

http://hdl.handle.net/10138/233755
https://doi.org/10.1037/com0000089

acceptedVersion

This is a post-peer-review, pre-copyedit version of an article published in Journal of Comparative Psychology, vol. 131, issue 4. The final authenticated version is available online at: https://doi.org/10.1037/com0000089.

Common Marmoset (*Callithrix jacchus*) Personality

Sonja E. Koski
University of Helsinki
Hannah M. Buchanan-Smith and Hayley Ash
University of Stirling
Judith M. Burkart
University of Zurich
Thomas Bugnyar
University of Vienna
Alexander Weiss
University of Edinburgh

Author Note

Sonja E. Koski, Department of Anthropology, University of Zurich; Hannah M. Buchanan-Smith and Hayley Ash, Behaviour and Evolution Research Group and Scottish Primate Research Group, Psychology, Faculty of Natural Sciences, University of Stirling; Judith M. Burkart, Department of Anthropology, University of Zurich; Thomas Bugnyar, Department of Cognitive Biology, University of Vienna; Alexander Weiss, Scottish Primate Research Group, School of Philosophy, Psychology and Language Sciences, Department of Psychology, The University of Edinburgh.

Please address correspondence concerning this article to: Sonja E. Koski, Centre of Excellence in Intersubjectivity in Interaction, Department of Social Sciences, University of Helsinki. Unioninkatu 35, 00014 Helsinki, Finland. E-mail: sonja.koski@helsinki.fi.

Abstract

Increasing evidence suggests that personality structure differs between species, but the evolutionary reasons for this variation are not fully understood. We built on earlier research on New World monkeys to further elucidate the evolution of personality structure in primates. We therefore examined personality in 100 family-reared adult common marmosets (*Callithrix jacchus*) from three colonies on a 60-item questionnaire. Principal components analyses revealed five domains that were largely similar to those found in a previous study on captive, ex-pet, or formerly laboratory-housed marmosets that were housed in a sanctuary. The interrater reliabilities of domain scores were consistent with the interrater reliabilities of domain scores found in other species, including humans. Four domains---conscientiousness, agreeableness, inquisitiveness, and assertiveness---resembled personality domains identified in other nonhuman primates. The remaining domain, patience, was specific to common marmosets. We used linear models to test for sex and age differences in the personality domains. Males were lower than females in patience, and this difference was smaller in older marmosets. Older marmosets were lower in inquisitiveness. Finally, older males and younger females had higher scores in agreeableness than younger males and older females. These findings suggest that cooperative breeding may have promoted the evolution of social cognition and influenced the structure of marmoset prosocial personality characteristics.

Keywords: marmoset, personality, primates, cooperative breeding

Introduction

Individuals of a species can be described by personality traits associated with dispersal, survival, offspring survival, cooperation, and cognitive ability (Sih & Del Giudice, 2012; Wolf & Weissing, 2012; Smith & Blumstein, 2008). Correlations among these traits are known as behavioral syndromes (Sih et al., 2004), evolutionary characters (Araya-Ajoy & Dingemanse, 2013), or personality components, factors, dimensions, or domains (Weiss & Adams, 2013). These correlations suggest that personality traits are manifestations of one or more underlying, latent processes. The species-specific personality structures defined by traits are then products of natural selection and mechanistic links that maintain the associations at species or population levels (e.g. Garamszegi et al., 2012; Dochtermann & Dingemanse, 2013). Comparing personality structures across species can reveal ecological and phylogenetic patterns of trait associations that hint at the functional bases of the traits (Gosling & Graybeal, 2007; Weiss & Adams, 2013).

Unfortunately, many animal personality studies focus on a small number of traits, such as aggression and boldness, and so an understanding of personality structure evolution is limited (Koski, 2014). Research on nonhuman primate personality bucks this trend (e.g., Koski, 2011a; Massen et al., 2013; Neumann et al., 2013; Konečná et al., 2008, 2012; Morton et al., 2013; Garai et al., 2016; Weiss et al., 2006, 2007, 2009, 2011, 2012a,b, 2015; Eckardt et al., 2015; Neumann et al., 2013; Adams et al., 2015; Uher & Visalberghi, 2016). Differences among species that are assessed on overlapping sets of traits are informative with respect to the evolution of personality structure (Gosling & Graybeal, 2007; Weiss & Adams, 2013). For example, in macaque species (Weiss et al., 2011; Adams et al., 2015), brown capuchin monkeys (Morton et al., 2013), and in mountain gorillas (Eckardt et al., 2015), traits related to gregariousness and sociopositive behavior define one factor, whereas they define two factors in chimpanzees (King & Figueredo, 1997), orangutans (Weiss et al., 2006), and in

humans (Costa & McCrae, 1992). On the other hand, in bonobos, most traits related to gregariousness and sociopositive behavior define a single factor, but a few related to gregariousness define a small additional factor (Weiss et al., 2015). These findings suggest that traits related to sociopositive behavior and gregariousness were fused in the common ancestor of platyrrhines and catarrhines, that the pattern in orangutans, chimpanzees, bonobos, and humans is derived, and that the bonobo pattern possibly represents a transitionary form, ancestral to African apes.

Personality studies of New World monkeys are a new direction for primate personality research (see, however, Byrne & Suomi, 2002), and have largely focused on capuchin monkeys (Morton et al., 2013; Manson & Perry, 2013; but see Santillan-Doherty et al., 2010 for spider monkeys, and Iwanicki & Lehmann, 2015; Šlipogor et al., 2016; and Koski & Burkart, 2015 for common marmosets). One reason for the burgeoning interest in studying New World monkey personality is that doing so helps to identify evolutionary scenarios that led to the emergence of personality structures. For example, by studying common marmosets, a cooperatively breeding species, one can determine whether and how cooperative breeding might influence the evolution of personality structure. Among cooperatively breeding species, some adults forgo breeding for several years and remain in the natal group to help carry, groom, and provision their infant siblings (Digby, 2007; Yamamoto et al., 2014). In primates, cooperative breeding has been associated with behavioral and cognitive characteristics, including increased social tolerance and proactive prosociality (Burkart et al., 2014; Schaffner & Caine, 2000), which facilitate performance in socio-cognitive tasks (Burkart & van Schaik, 2010, 2016). For example, like great apes and brown capuchin monkeys (Brosnan & de Waal, 2014; Anderson et al., 2013), common marmosets appear to be able to detect fairness in reciprocal third-party acts (Kawai et al., 2014). Moreover, although high reproductive skew leads to competition and occasionally

escalated aggression in Callitrichids (Schaffner & Caine, 2000; Digby et al., 2007; Yamamoto et al., 2014), aggression and conflict among individuals is infrequent and tends to not damage social relationships (Schaffner et al., 2005).

We assessed personality in common marmosets (*Callithrix jacchus*). Ours is not the first study of personality in a cooperatively breeding primate species. For one, humans are believed to be a cooperatively breeding species (Hrdy, 2009; Kramer, 2015), and have been the focus of the vast majority of personality research. One feature of human personality models, such as the Five-Factor Model (Costa & McCrae, 1992), is the absence of an independent personality domain related to competitive prowess. Instead, traits related to competitive prowess are found in the Five-Factor domains of extraversion, agreeableness, and neuroticism (Costa & McCrae, 1992; cf. Gosling & John, 1999). In contrast, traits related to assertiveness and competitive prowess form an independent personality domain in humans' closest living nonhuman relatives, chimpanzees (King & Figueredo, 1997) and bonobos (Weiss et al., 2015). Another feature of human personality is that agreeableness is defined by positive associations with traits related to helpfulness and prosociality and negative associations with traits related to aggression and competitiveness (Costa & McCrae, 1992). Its counterparts in chimpanzees (King & Figueredo, 1997; Freeman et al., 2013), bonobos (Weiss et al., 2015; Garai et al., 2016), orangutans (Weiss et al., 2006), and gorillas (Gold & Maple, 1994), on the other hand, are defined only by traits related to sociopositivity. These differences between the personality structures of humans and great apes suggest that a combination of high assertiveness and aggressiveness may be disadvantageous in cooperative breeders, and that combinations of sociopositive tendencies and low aggressiveness may be advantageous in cooperative breeders.

A recent study of common marmosets lent support to the possibility that certain combinations of traits may be selected for or against specifically due to cooperative breeding,

while other combinations may be due to a more general primate heritage. Iwanicki and Lehmann (2015) used ratings and behavioral observations to study marmoset personality. The ratings revealed an extraversion domain that resembled domains labeled confidence, dominance, or assertiveness that have been found in other nonhuman primate species (Freeman & Gosling, 2010), and conscientiousness and openness domains that resembled like-named domains in chimpanzees (King & Figueredo, 1997), humans (Costa & McCrae, 1992; Digman, 1990), and bonobos (Weiss et al., 2015). Additionally, they found an agreeableness domain that resembled its human counterpart, as it included positive loadings of prosocial traits and negative loadings of aggression. Moreover, Iwanicki and Lehmann's behavioral observations that revealed agreeableness, neuroticism, and perceptual sensitivity domains, showed that aggressive behavior was negatively correlated with agreeableness.

The identification of a conscientiousness domain in common marmosets is intriguing. To date, conscientiousness and similar domains, such as attentiveness, have only been identified in humans (Costa & McCrae, 1992), chimpanzees (King & Figueredo, 1997), bonobos (Weiss et al., 2015), and brown capuchin monkeys (Morton et al. 2013), all known for their advanced cognitive abilities. This finding is thus consistent with the hypothesis that cooperative breeding favored an increase of marmosets' cognitive skills, at least in the social domain, perhaps by selecting for increased social attentiveness (Burkart & van Schaik, 2016).

Our main aim was to further examine personality structure in common marmosets. To achieve this, we tested whether ratings of common marmosets on a broad questionnaire would yield evidence for domains resembling those uncovered by Iwanicki and Lehmann's (2015) study. Our sample differed from that of Iwanicki and Lehmann. The common marmosets in our sample were adults who had been parent-reared. Iwanicki and Lehmann's sample were former pets or former laboratory animals that were living in a sanctuary, and, furthermore, many had been hand- or foster-reared (35/63), and the sample included juveniles

(5/63) as well as adults. These differences are important. Pet monkeys often have abnormal rearing histories and hand-rearing is known to affect behavior (Soulsbury et al., 2009). Moreover, the curiosity and playfulness of juveniles may skew the personality profiles. As such, this study will show the degree to which the personality domains found by Iwanicki and Lehmann are not specific to their sample.

Our second aim was to examine sex- and age-differences in personality. Sex differences in mean trait level or syndrome structure are found in many species (e.g. Schuett & Dall, 2009; Michelangeli et al., 2016; Fresnau et al., 2014), including non-human primates (King et al., 2008) and humans (McCrae et al., 2005). Previous research has not found any differences between male and female common marmosets in experimentally assessed personality traits (Koski & Burkart, 2015; Šlipogor et al., 2016). However, females of this species have been described to be more responsive in contexts involving food (Box et al., 1997) and to explore novel objects in a foraging paradigm faster and more efficiently than males (Yamamoto et al., 2004). Moreover, the patterns of prosocial behavior differ between male and female helpers: in males, but not females, prosociality is higher in older, more experienced individuals (Burkart, 2015). This suggests that the previous studies may have failed to capture sex differences or that these differences are not reflected in repeatable personality traits.

Methods

Subjects

The subjects were 100 common marmosets that ranged in age from 2 to 14 years (M = 6.36, SD = 3.05). Of these subjects, 51 were males that ranged in age from 2 to 14 years (M = 6.02, SD = 3.03) and 49 females that ranged in age from 2 to 14 years (M = 6.71, SD = 3.06).

Housing and Husbandry

Subjects were housed at Dstl. Salisbury, United Kingdom, the University of Vienna,

Department of Cognitive Biology, Austria, and the University of Zürich, Anthropological Institute Primate Research Station, Switzerland. All subjects were born, reared, and housed in social groups. The study was approved after review by the Stirling University Psychology Ethics Committee and complies with legal and ethical requirements in the UK.

United Kingdom. This subsample included 51 subjects (25 males, 26 females) that were born at the facility. Twins and singletons were reared in their natal group, while triplets received supplementary feeding sessions for 2h twice per day for the first 8 weeks of life, spending the remainder of their time with the group. This practice has been shown to have little to no effect on neophobia, anhedonia, nor performance on cognitive bias tasks (Ash & Buchanan-Smith, 2016). Breeding marmosets (in groups of 2-10 individuals) were housed in one of three family rooms, each containing 8-12 groups of marmosets, in cages measuring 1.50m × 1.20m × 2.2m. Mixed-sex pairs were housed in one of three stock rooms, each containing 10-18 pairs, in wire cages measuring 1.0m × 0.60m × 1.80m. Cages were furnished with a nestbox, branches and logs, ropes, platforms, and perches, as well as suspended toys, including ladders, buckets, tea towels, hanging baskets, and food devices. Each family/pair also had access to a veranda. Temperature was thermostatically controlled at 23-24°C and humidity at 55% (range 45-65%), with lighting provided on a 12:12 h light:dark cycle. All marmosets had *ad libitum* access to water. Primate pellets were given between 08:00-09:00, and a variety of fruit was provided between 13:30 and 14:30. Malt loaf, egg, rusk, dates, peanuts, and bread were provided on alternate days. Gum arabic and banana milkshake were both given twice a week. Mealworms and forage mix were also scattered twice a week. Wet shavings were picked up each week, with a full cage clean every 8 weeks in breeding rooms, and every 4 weeks in stock rooms. Each marmoset was weighed once a month. New enrichment was provided once a week, including food parcels, boxes, and mealworm feeders. Each family had access to a ‘play cage’ for 3 days each, while stock pairs

were provided with a 'bug box'. Every animal was syringe trained once a month, and human socialization was carried out regularly. Housing and husbandry was in accordance with relevant national legislation.

The University of Vienna. This subsample included 21 subjects (12 males, 9 females) housed in 3 social groups consisting of a breeding pair and their offspring. All individuals were born in captivity and housed in their family groups. Every family group lived in a wire mesh indoor enclosure connected with a passageway system of tunnels with moveable doors to an outdoor enclosure (2.50 × 2.50 × 2.50 m indoors; 2.50 × 2.50 × 2.50 m outdoors). All enclosures had enrichment objects (branches, ropes, platforms, blankets, sleeping boxes, and tunnels), with wood shavings as floor bedding. An opaque plastic barrier prevented visual contact between adjacent family groups, while the groups remained in acoustic and olfactory contact. Daylight was the main source of lighting, but, because of the low amount of natural light in winter, lamps were maintained on a stable 12:12h light:dark cycle. In addition, one heating lamp per family group was always available on top of each enclosure. Temperature was maintained at 24-26°C and humidity was kept at 40-60%. All marmosets had *ad libitum* access to water and were fed every day at noon with a selection of marmoset pellets, fruits, vegetables, grains, milk products, marmoset jelly, protein and vitamin supplements, and insects. Several times per week monkeys received either a foraging box with mealworms or marmoset gum on the branches. The housing conditions were in accordance with Austrian legislation and the European Association of Zoos and Aquaria husbandry guidelines for Callitrichidae.

The University of Zurich. This subsample included 28 subjects (14 males, 14 females) housed in 6 social groups consisting of a breeding pair and 1 to 4 adult offspring. All individuals were born in the facility and reared by their natural parents in family groups. Subjects were housed in large indoor-outdoor enclosures comprising one or several basic

units (2m × 1m × 2m indoors; 2.75m × 1.70m or 2.50m × 2.40m outdoors). The enclosures included ropes, branches, and other enrichment devices, and were covered with natural bedding material. Both indoor and outdoor enclosures had heating lamps. Subjects had almost continuously free access to both enclosures, except during the necessary husbandry routines, at outside temperature < 5°C, and at night. They were fed three times a day with a diet of carbohydrate-rich mush enriched with vitamins and minerals, fruit, vegetables, gum, insects, boiled egg, and nuts. Water was available *ad libitum*. The housing conditions were in accordance with Swiss legislation and the European Association of Zoos and Aquaria husbandry guidelines for Callitrichidae.

Ratings

Eighteen researchers or animal keepers (6 in the United Kingdom, 5 in Austria, and 7 in Switzerland) with one to thirteen years of familiarity with the subjects rated the marmosets on a personality questionnaire. In the United Kingdom and in Switzerland, each subject was rated by 2 people, and in Austria, each subject was rated by 5 people.

The personality questionnaire consisted of 60 items. Each item consisted of an adjective paired with a brief definition that set it in the context of marmoset behavior (see Table S1). For example, the item 'helpful' was defined as "Monkey is willing to assist, accommodate to, or cooperate with other monkeys." Because of a clerical error, one item (unemotional) was included twice. For our analyses, we omitted ratings on the second occurrence of this item. Of the 59 items, 47 were taken from the Hominoid Personality Questionnaire[1] (Weiss et al., 2009), which, together with its predecessors (King & Figueredo, 1997; Weiss et al., 2006), and offshoots (Konečná et al., 2008, 2012; Iwanicki & Lehman, 2015), has been used to assess personality in several nonhuman primate species (Weiss, 2017). A further 12 items were taken from a questionnaire used to study Hanuman langurs (Konečná et al., 2008) and Barbary macaque personality (Konečná et al., 2012).

The instructions on the questionnaire asked raters to judge subjects based on their overall impressions of that monkey, to assign a rating of 1 (absence of a trait) to 7 (extreme presence of a trait) for each trait, and to not discuss their ratings with other raters. To minimize misunderstandings by German-speaking raters in Austria and Switzerland, we translated the questionnaire into German and the raters had the forms available in both languages at all times.

Analyses

We used two intraclass correlations (*ICC*s) to determine how consistent raters were in their ratings of each item. The first of these, *ICC*(3,1), indicates the reliability of ratings by any single judge. The second, *ICC*(3,*k*), measures the reliability of the mean rating of *k* judges (Shrout & Fleiss, 1979).

As in previous studies (e.g. Morton et al., 2013), for reliable items, we used principal components analysis to examine the personality structure of the mean ratings across all raters. To determine how many components to extract, we inspected the scree plot and used parallel analysis (Horn, 1965). We then subjected our components to an orthogonal (varimax) and oblique (promax) rotation. If the varimax and promax rotations yielded similar components and the interfactor correlations were modest, we interpreted the varimax rotation. If the two rotations yielded different components or the inter-factor correlations were moderate to large, we interpreted the promax rotation.

We then computed unit-weighted component scores (Gorsuch, 1984) to be used in our final analyses. This involved our assigning weights of 0 to component loadings less than |0.4|, weights of +1 to component loadings greater than or equal to 0.4, and weights of -1 to component loadings that were less than or equal to -0.4. In the event that an item had multiple loadings greater than or equal to |0.4| we assigned the weight to the component on which the item had the highest absolute loading. We then transformed these raw unit-weighted scores

into z-scores (mean = 0, SD = 1). In the first of the two final analyses we ascertained the interrater reliabilities of the domains, again using *ICC*(3,1) and *ICC*(3,*k*). In the second of these analyses we used five multiple regressions (one for each personality domain) to test for sex and age effects. Here the component score was the dependent variable and the independent variables were sex (-1 for females, +1 for males), age (mean centered), and a product term representing the sex × age interaction.

We conducted all analyses using version 3.3.2 of R (R Core Team, 2016). Parallel analysis and principal components analysis were conducted using the fa.parallel and principal functions from the psych package (Revelle, 2015), respectively. Multiple regressions were conducted using the lm function.

Results

Out of Range and Missing Data

One rater of one marmoset in Austria assigned a "0" to a single item and 5 raters of 24 marmosets in the United Kingdom assigned a "0" to up to 12 ratings, each. Combined, across 25 marmosets, 90 items were assigned a rating of "0". We assigned a "1" to these ratings. In addition, for the marmosets housed in the United Kingdom, one rater did not rate two marmosets on a single trait, each, a second did not rate one marmoset on a single trait, and a third did not rate three marmosets on a single trait, each, and one marmoset on two traits. For the marmosets housed in Austria, one rater did not rate two marmosets on a single trait, each. For the marmosets housed in Switzerland, one rater did not rate one marmosets on two traits. In all 12 of these cases we substituted the mean value of the trait across all marmosets in the study.

Item Interrater Reliabilities

The interrater reliabilities for all the items are available in Table S2. The interrater reliabilities of the items 'manipulative' and 'conventional' were below 0. *ICC*(3,1) estimates

for the remaining items ranged from 0.01 for ‘popular’ to 0.37 for ‘gentle’, and the mean and standard deviation of the *ICC*(3,1) estimates for these items were 0.20 and 0.09, respectively. The interrater reliabilities of single ratings were lower but within the range of those in studies of humans and other species (Morton et al., 2013; Weiss et al., 2011, 2015; Mõttus et al., 2017) and considered as acceptable (e.g. Mõttus et al., 2014). *ICC*(3,*k*) estimates for the items with reliabilities greater than 0 ranged from 0.03 for ‘popular’ to 0.60 for ‘gentle’ and the mean and standard deviation of the *ICC*(3,*k*) estimates for these items were 0.38 and 0.14, respectively. Note, that *ICC*(3,*k*) estimates are not typically compared between studies because they will, in part, vary as a function of how many raters there were per subject whereas *ICC*(3,1) estimates do not.

Personality Structure

Parallel analysis and examination of the scree plot indicated that there were five components with eigenvalues equal to 16.09, 8.04, 4.84, 4.13, and 2.71, which accounted for 63% of the variance. To be certain that the five-component solution was best we also extracted six components (see Tables S3 and S4). The sixth component had an eigenvalue of 1.84. After applying a varimax rotation, only the items ‘selective’ and ‘stingy’ had unique, salient loadings on that component (0.50 and 0.49, respectively). After applying a promax rotation, only the items ‘selective’, ‘stingy’, and ‘alert’ had unique, salient loadings on that component (0.53, 0.52, and -0.40, respectively). The sixth component was thus uninterpretable and so we retained a five-component solution.

For the five-component solution, because there were only minor differences between varimax and promax solutions (all congruence coefficients ≥ 0.97) and the absolute correlations between components were modest (range = 0.03 to 0.39, $M = 0.13$, $SD = 0.12$), we retained the varimax-rotated solution (see Table S5 for the promax-rotated solution and the correlations between components). Finally, we compared the five varimax-rotated

components to five varimax-rotated factors (see Table S6). The component and factor structures were virtually identical (all congruence coefficients ≥ 0.99).

The five varimax-rotated components are presented in Table 1. For ease of interpretation, we reflected the first, third, and fifth components by multiplying loadings by -1. The first component resembled conscientiousness domains found in common marmosets (Iwanicki & Lehmann, 2015), chimpanzees (King & Figueredo, 1997; Weiss et al., 2007; Weiss et al., 2009; King et al., 2005), and bonobos (Weiss et al., 2015), though it was broader than the chimpanzee and bonobo conscientiousness domains as it also encompassed traits related to play behavior. This component thus described differences in low antagonism, high self-control, and low playfulness, and we therefore named it 'conscientiousness'.

The second component described high levels of sociopositive and prosocial traits, and thus was a mix of traits related to the extraversion and agreeableness domains in humans (Costa & McCrae, 1992), chimpanzees (King & Figueredo, 1997), and orangutans (Weiss et al., 2006). Similar to the agreeableness domain found by Iwanicki and Lehmann (2015), this component included negative loadings of socio-negative traits such as 'aggressive' and 'irritable'. Thus, it differed from bonobo agreeableness (Weiss et al., 2015), brown capuchin monkey sociability (Morton et al., 2013), and the friendliness domain found in various macaque species (Adams et al., 2015; Weiss et al., 2011). In light of these comparisons, we named this component 'agreeableness'.

The third component was defined by loadings on items related to assertiveness, dominance, such as a positive loading of 'dominant' and a negative loading of 'submissive', but also by negative loadings on traits related to anxiety, vulnerability, and vigilance, such as 'fearful' and 'cautious'. This component was thus similar to the extraversion domain found in the previous study of marmosets (Iwanicki & Lehmann, 2015) and domains labeled dominance, confidence, and assertiveness in other nonhuman primate species (Freeman &

Gosling, 2010). We thus named this component ‘assertiveness’.

The fourth component was characterized by items related to attentiveness in brown capuchin monkeys (Morton et al., 2013) and in bonobos (Weiss et al., 2015). For example, ‘patient’ had a positive loading on this component and ‘distractible’ had a negative loading on this component. It also included positive loadings from items related to sociopositive behaviors, such as ‘sensitive’ and ‘sympathetic’, and problem solving, such as ‘inventive’ and ‘intelligent’. This component is thus different from the domains identified by Iwanicki and Lehmann (2015) and appears to not have been found in other nonhuman primates. We tentatively named this component ‘patience’.

The fifth component was characterized by positive and negative loadings of traits related to activity, such as ‘active’ and ‘lazy’, respectively, positive loadings on traits related to exploratory behavior, such as ‘inquisitive’, a negative loading on ‘solitary’, and a positive loading on a trait related to vigilance (‘alert’). It thus strongly resembled the openness domain identified by Iwanicki and Lehmann (2015). It also resembles the orangutan extraversion domain (Weiss et al., 2006), which was characterized by traits related to gregariousness and exploratory behavior. We named this component ‘inquisitiveness’.

Component Interrater Reliabilities

The interrater reliabilities of individual ratings for conscientiousness, sociability, assertiveness, patience, and inquisitiveness were 0.41, 0.44, 0.32, 0.39, and 0.26, respectively, and thus comparable to those derived in humans (McCrae & Costa, 1987) and in nonhuman primates (Weiss et al., 2011, 2015). The interrater reliabilities of mean ratings for these components were 0.65, 0.68, 0.56, 0.63, and 0.48, respectively.

Sex and Age Effects

The effects of sex, age, and the sex × age interaction are presented in Table 2. For conscientiousness, males were lower than females, but this effect was negligible and not

significant. Moreover, older subjects were lower in conscientiousness, but this effect was not significant. The sex × age interaction was also not significant.

For agreeableness, males were slightly higher than females and older subjects were higher in sociability, but neither of these effects was significant. There was a significant sex × age interaction: among males, older subjects were higher in agreeableness whereas among females, younger individuals were higher in agreeableness (b = 0.07, 95% CI = 0.03, 0.01, p = 0.029). However, given the number of statistical tests and the non-significant sex and age effects, this effect may be a false positive and should be treated with caution.

For assertiveness, males and older subjects scored lower than females and younger subjects, respectively, but neither of these effects were significant. The sex × age interaction was also not significant.

For patience, males scored significantly lower than females (b = -0.30, 95% CI = -0.48, -0.11, p = 0.002). Although older subjects were lower in patience, the effect of age was not significant. There was, however, a significant sex × age interaction indicating that the difference between males and females was smaller among older subjects (b = 0.07, 95% CI = 0.01, 0.14, p = 0.020).

For inquisitiveness, males and older subjects were lower, but only the effect of age was significant (b = -0.13, 95% CI =-0.19, -0.07, p < 0.001). The sex × age interaction was not significant.

Discussion

We asked individuals familiar with 100 common marmosets to rate them on 59 personality traits. Their ratings revealed five domains---conscientiousness, agreeableness, assertiveness, patience, and inquisitiveness---that resembled domains found in a previous study of common marmosets (Iwanicki & Lehmann, 2015).

Conscientiousness resembled domains found in humans (Digman, 1990; Costa &

McCrae, 1992) and in cognitively advanced nonhuman primates, such as chimpanzees (King & Figueredo, 1997), brown capuchin monkeys (Morton et al., 2013), and bonobos (Weiss et al., 2015). As such, this finding supports Iwanicki and Lehmann's (2015) finding in marmosets, and indicates that marmosets have relatively advanced cognitive skills. Particularly social cognition is advanced in marmosets. It may be favored due to the need for increased social attentiveness and tolerance, as cooperative breeding requires an ability to coordinate cooperative actions and to pay attention to others' actions and needs (Burkart & van Schaik, 2010, 2016).

Assertiveness resembled domains found in several nonhuman primate species (Freeman & Gosling, 2010) and corroborated Iwanicki and Lehmann's (2015) earlier finding of a personality domain related to dominance in common marmosets. This finding lends further support to the notion that domains like dominance, confidence, or assertiveness are universal features of personality in nonhuman primates (see, e.g., Freeman & Gosling, 2010). Apparently, the association of traits related to assertiveness and boldness is not selected against in marmosets. Thus, cooperative breeding has perhaps not been the main driver of the human pattern, where traits associated with assertiveness are found within the extraversion, agreeableness, and neuroticism domains.

Inquisitiveness captured an association of curiosity, activity, exploration, and vigilance. It was thus like the openness domain in the study of marmosets by Iwanicki and Lehmann (2015), and resembled the openness domain in brown capuchin monkeys (Morton et al., 2013). Similar domains that capture the association of activity and exploratory tendency have been identified in Old World monkeys, including vervet monkeys (McGuire et al, 1994) and rhesus macaques (Weiss et al., 2011), and in great apes, including chimpanzees (King & Figueredo, 1997; Weiss et al., 2007, 2009) and bonobos (Weiss et al. 2015). As such, it is likely that this domain may also be a universal primate personality domain. In

contrast, we did not find anything resembling the perceptual sensitivity domain, which captured activity, vigilance, and time spent foraging relative to feeding, that was identified using behavioral data (Iwanicki & Lehmann, 2015). Interestingly, in the Iwanicki & Lehmann's (2015) study the items vigilance and activity were captured by the openness domain, as was the case in our study, but openness did not correlate with perceptual sensitivity. This suggests that the behavioral measures of activity and vigilance are not assessing the same constructs as are ratings of those items. Therefore, in the future studies it would be useful to assess the criterion validity of the openness and vigilance related items and behaviors (see below) and address the implication of such differences between the methods.

Of the remaining domains, agreeableness encompassed mostly prosocial personality characteristics and, negatively, loadings on traits related to aggression. This finding supports further the similarity in marmoset and human agreeableness identified earlier by Iwanicki and Lehmann (2015), and implies that sociopositive traits of gregariousness and prosociality associated with low aggressiveness may be adaptive in cooperative breeders.

Finally, the patience domain appeared to be unique to common marmosets. It included characteristics related to a socio-positive orientation, attentiveness, inventiveness, and focus. The existence of this domain, then, suggests that there was selection for a positive correlation between prosocial traits and traits related to persistence and cognitive performance. However, the agreeableness domain also captured prosocial traits, thus, socio-positive and helpful characteristics are not unidimensional in marmosets. One possibility is that the patience domain is akin to the "helping syndrome", i.e., the positive association of repeatable prosocial behaviors directed to offspring, found in mongooses (*Mungos mungo*) and meerkats (*Suricata suricatta*). However, in marmosets, the prosocial characteristics in patience are not those related to actual helping, which are found in agreeableness, but those related to

discerning others' needs and responding to them kindly.

Another possibility is that feeding ecology may have led to the emergence of a patience domain. Feeding ecology has proven an important driver of behavioral and brain evolution in nonhuman primates (e.g. DeCasien et al., 2017; MacLean et al., 2014). For marmosets, one possibility is that the evolution of the patience domain was favored by gum feeding, namely as gum is an embedded food source and takes time and effort to extract. Such a foraging strategy may promote cognition and curiosity (Burkart et al, 2016; Schuppli et al., 2016, Stevens et al. 2005). Extractive foraging is suggested to favor an association of exploration tendency and persistence (Massen et al., 2013). In our study we found that, although inquisitiveness and patience domains were not correlated (Table S5), two traits that defined inquisitiveness, 'exploratory' and 'inquisitive', had strong loadings on patience, too. Another possibility is that the patience domain emerged in response to insectivory. Flushing out insects and capturing fast moving prey presumably requires inquisitiveness and patience, respectively. To test which of these hypotheses is supported requires a phylogenetic analysis of primate and non-primate species that differ in their socioecologies and feeding ecologies, that have been assessed on a large number of traits. However, the proposed hypotheses need not be mutually exclusive, as marmoset prosociality entails proactive food sharing (Burkart et al., 2007, 2014), so both obtaining and provisioning food items may favor the positive associations of traits found in the patience domain.

In sum, the present findings mostly resemble those in a previous study of common marmosets (Iwanicki & Lehmann, 2015), despite the marmosets in the current study having different rearing histories and being rated by a somewhat different and much longer questionnaire. Although there were also differences in cage size and complexity in the current study, which may affect behavior (Kitchen & Martin, 1995: common marmosets), it is unlikely that the smaller cages of the UK colony influenced personality significantly, as these

were still relatively large, enriched enclosures allowing opportunities for natural behavior. As such, this study supports the generalizability of personality structure in humans (McCrae et al., 2005) and in chimpanzees (Dutton, 2008; King et al., 2005; Weiss et al., 2007, 2009; Freeman et al., 2013) across different samples. We also found that cooperative breeding may have led to a conscientiousness-like domain in common marmosets, which may be related to cooperative breeding affecting the evolution of increased social attention and cognition. Further, we hypothesize that cooperative breeding may have promoted an inverse association between aggression and prosociality in humans, as we found a similar pattern in marmosets. Finally, we hypothesize that cooperative breeding may have led to the emergence of a unique patience domain in common marmosets. To test these hypotheses, further, comparative studies of callitrichids and more generally, cooperatively breeding primates, are warranted. It would be particularly beneficial if the studies would also include behavioral measures and experiments to complement the questionnaires.

Iwanicki and Lehmann (2015) found evidence of agreement between behavioral and rated measures, most strongly concerning rated agreeableness and the behavioral measures of prosociality and aggression. In contrast, openness and assertiveness, which were obtained from ratings, were not correlated with any behavioral measures, bar play and self-grooming. Several studies on other primate species have assessed the construct validity of questionnaires (Pederson et al., 2005; Morton et al., 2013; Konečná et al., 2012; Uher & Asendorpf, 2008; Freeman et al., 2013), and the results are mixed with some, but not all, constructs showing correlations between conceptually similar behavioral measures of the same animals. Correspondence of rated components and measured behaviors tends be better in studies on ape personality (Eckardt et al., 2015; Pederson et al., 2005; Freeman et al., 2013). As has been discussed elsewhere (e.g., Uher, 2008; Uher et al., 2008; Koski, 2011b), this may be because the rating method depends on the degree to which people can intuitively aggregate

the study species' behavior into meaningful categories. This may be more difficult for species that are taxonomically distant from humans; however, at least in primates, the structures derived using behavioral measures and ratings are often highly similar (compare, for example, Table 3 in Neumann et al., 2013 and Table S6 in Adams et al., 2015 or Table 6 in Morton et al., 2013 and Table 3 in Uher & Visalberghi, 2016). Moreover, construct validation typically is post-hoc without predictions of the expected correlations (but see Eckardt et al., 2015 and Uher et al., 2008). We thus urge future researchers to *a priori* consider what correlations one should and should not expect based on the functions of these behaviors in the species of interest.

We found few age- or sex-related differences in the component scores. Inquisitiveness was lower in older individuals, which is consistent with findings in, for example, chimpanzees (Massen et al., 2013) and humans (Roberts et al., 2006). We also found a significant sex by age interaction for agreeableness: older males and younger females had higher scores than younger males and older females. This result is consistent with sex differences in the amount of prosocial behavior in male and female helpers: rearing experience and age increase proactive behavior in male and decrease it in female helpers (Burkart, 2015). These patterns are probably related to the fact that, among callithrichids, female helpers are more likely to disperse as they get older whereas males are more likely to inherit the breeding position in their natal groups (Yamamoto et al., 2014).

Conclusion

We found that marmosets present three personality domains like those in other primates, that is, agreeableness, assertiveness, and inquisitiveness, a conscientiousness domain that has been found in great apes and brown capuchin monkeys in addition to marmosets, and a domain, patience, that may have come about via selection for correlations between traits related to prosociality, intelligence, and persistence. Together, these findings

suggest that the selection pressures related to cooperative breeding may have influenced personality evolution in this species.

Acknowledgements

We thank the staff at the three facilities (Dstl. Salisbury, UK; Zurich University Primate Station, Switzerland, and Vienna University Cognitive Biology primate facility, Austria) for their assistance with the research and dedicated care of the marmosets. We are grateful to all those who completed the questionnaires, namely: Michèle Schubiger, Christa Finkenwirth, Eloisa Martins, Heinz Galli, Thomas Bischof, Alexandra Christian, Caecilia Faltin, Martina Schiestl, Tina Gunhold, and Vedrana Šlipogor. We are grateful to Doree Fragazy and the three anonymous reviewers for their helpful comments that greatly improved the manuscript. HA was funded by a studentship awarded by the NC3Rs.

References

Adams, M. J., Majolo, B., Ostner, J., Schülke, O., De Marco, A., Thierry, B., Engelhardt, A., Widdig, A., Gerald, M.S., & Weiss, A. (2015). Personality structure and social style in macaques. *Journal of Personality and Social Psychology*, *109*, 338-353.

Anderson, J. R., Takimoto, A., Kuroshima, H., & Fujita, K. (2013). Capuchin monkeys judge third-party reciprocity. *Cognition, 127,* 140-146.

Anestis, S. F. (2005). Behavioral style, dominance rank, and urinary cortisol in young chimpanzees (*Pan troglodytes*). *Behaviour*, *142*, 1251-1274.

Araya-Ajoy, Y. G., & Dingemanse, N. J. (2014). Characterizing behavioural "characters": an evolutionary framework. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20132645-20132645.

Ash, H., & Buchanan-Smith, H. M. (2016). The long-term impact of infant rearing background on the affective state of adult common marmosets (*Callithrix jacchus*). *Applied Animal Behaviour Science*, *174*, 128-136.

Box, H. O. (1997). Foraging strategies among male and female marmosets and tamarins (Callitrichidae): New perspectives in an underexplored area. *Folia Primatologica, 68,* 296-306.

Brosnan, S. F., & de Waal, F. B. M. (2014). Evolution of responses to (un)fairness. *Science*, *346*, 1251776-1251776.

Burkart, J. (2015). Opposite effects of male and female helpers on social tolerance and proactive prosociality in callitrichid family groups. *Scientific Reports, 5*, 1-9.

Burkart, J. M., & van Schaik, C. P. (2010). Cognitive consequences of cooperative breeding in primates? *Animal Cognition*, *13* 1-19.

Burkart, J. M., & Van Schaik, C. P. (2016). Revisiting the consequences of cooperative breeding. *Journal of Zoology, 299,* 77-83.

Burkart, J. M., Fehr, E., Efferson, C., & van Schaik, C. P. (2007). Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences*, 104, 19762-19766.

Burkart, J. M., Allon, O., Amici, F., Fichtel, C., Finkenwirth, C., Heschl, A., Huber, J., Isler, K., Kosonen, Z.K., Martins, E., Meulman, E.J. ,Richiger, R. Rueth, K., Spillmann, B., Wiesendange, S., & van Schaik, C.P. (2014). The evolutionary origin of human hyper-cooperation. *Nature Communications*, *5*, 4747.

Byrne, G., & Suomi, S. J. (2002). Cortisol reactivity and its relation to homecage behavior and personality ratings in tufted capuchin (*Cebus paella*) juveniles from birth to six years of age.

Psychoneuroendocrinology, 27, 139-154.

Carter, A. J., English, S., & Clutton-Brock, T. H. (2014). Cooperative personalities and social niche specialization in female meerkats. *Journal of Evolutionary Biology*, *27*, 815-825.

Costa, P. T., Jr. & McCrae, R. R. (1992). Four ways five factors are basic. *Personality and Individual Differences, 13*, 653-665.

DeCasien, A. R., Williams, S. A., & Higham, J. P. (2017). Primate brain size is predicted by diet but not sociality. *Nature Ecology & Evolution*, *1*, 1–7. http://doi.org/10.1038/s41559-017-0112

Digby, L. J., Ferrari, S. F., & Saltzman, W. (2007). *Callitrichines: the role of competition in cooperatively breeding species*. In Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M.A., Bearder, S.K. (Eds.), Primates in Perspective (pp. 85–105). New York: Oxford University Press.

Digman, J. M. (1990). Personality structure: Emergence of the Five-Factor Model. *Annual Review of Psychology, 41,* 417-440.

Dochtermann, N. A., & Dingemanse, N. J. (2013). Behavioral syndromes as evolutionary constraints. *Behavioral Ecology*, *24*, 806-811.

Dutton, D. M. (2008). Subjective assessment of chimpanzee (*Pan troglodytes*) personality: Reliability and stability of trait ratings. *Primates, 49*, 253-259.

Eckardt, W., Steklis, H. D., Steklis, N. G., Fletcher, A. W., Stoinski, T. S., & Weiss, A. (2015). Personality dimensions and their behavioral correlates in wild Virunga mountain gorillas (*Gorilla beringei beringei*). *Journal of Comparative Psychology*, *129*, 26-41.

English, S., Nakagawa, S., & Clutton-Brock, T. H. (2010). Consistent individual differences in cooperative behaviour in meerkats (*Suricata suricatta*). *Journal of Evolutionary Biology*, *23*, 1597-1604.

Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: A review and evaluation of past research. *American Journal of Primatology, 71*, 1-19.

Freeman, H. D., Brosnan, S. F., Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Gosling, S. D. (2013). Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using a simultaneous top-down/bottom-up design. *American Journal of Primatology*, *75*, 1042-1053.

Fresneau, N., Kluen, E., & Brommer, J. E. (2014) A sex-specific behavioral syndrome in a wild passerine. *Behavioural Ecology 25,* 359–367.

Garai, C., Weiss, A., Arnaud, C., & Furuichi, T. (2016). Personality in wild bonobos (*Pan paniscus*). *American Journal of Primatology*, *78*, 1178-1189.

Garamszegi, L. Z., Markó, G., & Herczeg, G. (2012). A meta-analysis of correlated behaviours with implications for behavioural syndromes: mean effect size, publication bias, phylogenetic effects and the role of mediator variables. *Evolutionary Ecology*, *26*, 1213-1235.

Gold, K. C., & Maple, T. L. (1994). Personality assessment in the gorilla and its utility as a management tool. *Zoo Biology, 13,* 509-522.

Gorsuch, R. L. (1984). *Factor analysis*. Hillsdale, NJ: Lawrence Erlbaum Associates.

Gosling, S. D., & Graybeal, A. (2007). Tree thinking: A new paradigm for integrating comparative data in psychology. *The Journal of General Psychology*, *134*, 259-277.

Horn, J. L. (1965). A rationale and test for the number of factors in factor analysis. *Psychometrika, 30,* 179-185.

Hrdy, S. B. (2009). Mothers and others. The evolutionary origins of mutual understanding. Cambridge MA: Belknap Press.

Iwanicki, S., & Lehmann, J. (2015). Behavioral and trait rating assessments of personality in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology*, *129*, 205-217.

Kawai, N., Yasue, M., Banno, T., & Ichinohe, N. (2014). Marmoset monkeys evaluate third-party reciprocity. *Biology Letters*, *10*, 20140058–20140058.

King, J. E., & Figueredo, A. J. (1997). The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality*, *31*, 257-271.

King, J. E., Weiss, A., & Farmer, K. H. (2005). A chimpanzee (Pan troglodytes) analogue of cross-national generalization of personality structure: Zoological parks and an African sanctuary. *Journal of Personality, 73,* 389-410.

Kitchen, A. M., & Martin, A. A. (1995). The effects of cage size and complexity on the behavior of captive common marmosets (*Callithrix jacchus jacchus*). *Laboratory Animals, 30, 317-326.*

Konečná, M., Lhota, S., Weiss, A., Urbánek, T., Adamová, T., & Pluháček, J. (2008). Personality in free-ranging Hanuman langur (*Semnopithecus entellus*) males: Subjective ratings and recorded behavior. *Journal of Comparative Psychology*, *122*, 379-389.

Konečná, M., Weiss, A., Lhota, S., & Wallner, B. (2012). Personality in Barbary macaques (*Macaca sylvanus*): Temporal stability and social rank. *Journal of Research in Personality*, *46,* 581-590.

Koski, S. E. (2011a). Social personality traits in chimpanzees: Temporal stability and structure of behaviourally assessed personality traits in three captive populations. *Behavioral Ecology and Sociobiology*, *65*, 2161-

626 2174.
627 Koski, S. E. (2011b). How to measure animal personality and why does it matter? Integrating the psychological
628 and biological approaches to animal personality. In M. Inoue-Murayama., S. Kawamura. & A. Weiss (Eds.)
629 From Genes to Animal Behavior (pp. 115–136). Tokyo: Springer.
630 Koski, S. E. (2014). Broader horizons for animal personality research. *Frontiers in Ecology and Evolution*, *2*, 1-
631 6.
632 Koski S. E., & Burkart, J. M. (2015). Common marmosets show social plasticity and group-level similarity in
633 personality. *Scientific Reports*, *5*, 8878.
634 Kramer, K. L. (2015). Cooperative breeding and human evolution. Emerging Trends in Social and Behavioral
635 Sciences: An interdisciplinary, searchable, and linkable resource. 1-13.
636 MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., et al. (2014). The evolution of
637 self-control. *Proceedings of the National Academy of Sciences*, 111, E2140–E2148.
638 Manson, J. H., & Perry, S. (2013). Personality structure, sex differences, and temporal change and stability in
639 wild white-faced capuchins, *Cebus capucinus*. *Journal of Comparative Psychology, 127,* 299-311
640 Massen, J. J. M., Antonides, A., Arnold, A.-M. K., Bionda, T., & Koski, S. E. (2013). A behavioral view on
641 chimpanzee personality: Exploration tendency, persistence, boldness, and tool-orientation measured with
642 group experiments. *American Journal of Primatology*, *75*, 947-958.
643 McCrae, R. R., & Costa, P. T., Jr. (1987). Validation of the five-factor model of personality across instruments
644 and observers. *Journal of Personality and Social Psychology*, *52*, 81-90.
645 McCrae, R. R., Terracciano, A., & 78 members of the personality profiles of cultures project. (2005). Universal
646 features of personality traits from the observer's perspective: Data from 50 cultures. *Journal of Personality*
647 *and Social Psychology, 88*, 547-561.
648 McGuire, M. T., Raleigh, M. J., & Pollack, D. B. (1994). Personality features in vervet monkeys: The effects of
649 sex, age, social status, and group composition. *American Journal of Primatology*, *33*, 1–13.
650 Michelangeli, M., Chapple, D. G., & Wong, B. B. M. (2016). Are behavioural syndromes sex specific?
651 Personality in a widespread lizard species. *Behavioral Ecology and Sociobiology*, *70, 1911-1919.*
652 Morton, F. B., Lee, P. C., Buchanan-Smith, H. M., Brosnan, S. F., Thierry, B., Paukner, A., de Waal, F. B.
653 M., Widness, J., Essler, J. L., & Weiss, A. (2013). Personality structure in brown capuchin monkeys
654 (*Sapajus apella*): Comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo spp*.), and rhesus
655 macaques (*Macaca mulatta*). *Journal of Comparative Psychology*, *127*, 282-298.

Mõttus, R., Kandler, C., Bleidorn, W., Riemann, R., & McCrae, R. R. (2017). Personality traits below facets: The consensual validity, longitudinal stability, heritability, and utility of personality nuances. *Journal of Personality and Social Psychology*, *112*, 474-490.

Mõttus, R., McCrae, R. R., Allik, J., & Realo, A. (2014). Cross-rater agreement on common and specific variance of personality scales and items. *Journal of Research in Personality*, *52*, 47–54.

Neumann, C., Agil, M., Widdig, A., & Engelhardt, A. (2013). Personality of wild male crested macaques (*Macaca nigra*). *PloS One, 8:* e69383.

Pederson, A. K., King, J. E., & Landau, V. I. (2005). Chimpanzee (*Pan troglodytes*) personality predicts behavior. *Journal of Research in Personality*, *39*, 534-549.

Revelle, W. (2015). Package 'psych'. Retrieved 7th November 2016 from https://cran.r-project.org/web/packages/psych/psych.pdf

Roberts, B. W., Walton, K. E., & Viechtbauer, W. (2006). Patterns of mean-level change in personality traits across the life course: A meta-analysis of longitudinal studies. *Psychological Bulletin*, *132*, 1–25.

Sanderson, J. L., Stott, I., Young, A. J., Vitikainen, E. I. K., Hodge, S. J., & Cant, M. A. (2015). The origins of consistent individual differences in cooperation in wild banded mongooses, *Mungos mungo*. *Animal Behaviour*, *107*(C), 193-200.

Santillán-Doherty, A. M., Cortés-Sotres, J., Arenas-Rosas, R. V., Márquez-Arias, A., Cruz, C., Medellín, A., Aguirre, M., Muñóz-Delgado, J., & Díaz, J. L. (2010). Novelty-seeking temperament in captive stumptail macaques (*Macaca arctoides*) and spider monkeys (*Ateles geoffroyi*). *Journal of Comparative Psychology*, *124*, 211-218.

Schaffner, C. M., & Caine, N. G. (2000). The peacefulness of cooperatively breeding partners. In F, Aureli & F. B. M. de Waal (Eds.) *Natural Conflict Resolution* (pp155-169). Berkeley: University of California Press.

Schaffner, C. M., Aureli, F., & Caine, N. G. (2005). Why small groups of tamarins do not reconcile conflicts. *Folia Primatologica*, *76*, 67-76.

Schuett, W., & Dall, S. R. X. (2009). Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, *77*, 1041–1050.

Schuett, W., Tregenza, T., & Dall, S. R. X. (2010). Sexual selection and animal personality. *Biological Reviews*, *85*(2), 217–246.

Schuppli, C., Graber, S. M., Isler, K., & van Schaik, C. P. (2016). Life history, cognition and the evolution of complex foraging niches. *Journal of Human Evolution*, *92*(C), 91–100.

Shrout, P. E., & Fleiss, J. L. (1979). Intraclass correlations: Uses in assessing rater reliability. *Psychological Bulletin, 86,* 420-428.

Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: A behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 2762-2772.

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology and Evolution. 19,* 372 - 378.

Šlipogor, V., Gunhold-de Oliveira, T., Tadić, Z., Massen, J. J. M., & Bugnyar, T. (2016). Consistent inter-individual differences in common marmosets (*Callithrix jacchus*) in Boldness-Shyness, Stress-Activity, and Exploration-Avoidance. *American Journal of Primatology, 78,* 1–13.

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology, 19*, 448-455.

Soulsbury, C. D., Iossa, G., Kennell, S. & Harris, S. (2009). The welfare and suitability of primates kept as pets. *Journal of Applied Animal Welfare Science*, *12*, 1-20.

Stevens, J. R., Hallinan, E. V., & Hauser, M. D. (2005). The ecology and evolution of patience in two New World monkeys. *Biology Letters*, *1*(2), 223-226.

Uher, J. (2008). Comparative personality research: Methodological approaches. *European Journal of Personality*, *22*, 427-455.

Uher, J., & Asendorpf, J. B. (2008). Personality assessment in the Great Apes: Comparing ecologically valid behavior measures, behavior ratings, and adjective ratings. *Journal of Research in Personality*, *42*, 821–838.

Uher, J., & Visalberghi, E. (2016). Observations versus assessments of personality: A five-method multi-species study reveals numerous biases in ratings and methodological limitations of standardised assessments. *Journal of Research in Personality*, *61*, 61-79.

Uher, J., Asendorpf, J. B., & Call, J. (2008). Personality in the behaviour of Great Apes: Temporal stability, cross-situational consistency and coherence in response. *Animal Behaviour*, *75*, 99-112.

Weiss, A. (2017). Exploring factor space (and other adventures) with the Hominoid Personality Questionnaire. In J. Vonk, A. Weiss, & S. Kuczaj (Eds.), Personality in Nonhuman Animals. Springer.

Weiss, A., & Adams, M. J. (2013). Differential behavioral ecology: The structure, life history, and evolution of animal personality. In C. Carere & D. Maestripieri (Eds.) *Animal Personalities. Behavior, physiology, and evolution* (pp. 96-123). Chicago: University of Chicago Press, Chicago.

Weiss, A., Adams, M. J., Widdig, A., & Gerald, M. S. (2011). Rhesus macaques (*Macaca mulatta*) as living

716 fossils of hominoid personality and subjective well-being. *Journal of Comparative Psychology*, *125*, 72-83.

717 Weiss, A., Gartner, M. C., Gold, K. C., & Stoinski, T. S. (2012a). Extraversion predicts longer survival in

718 gorillas: An 18-year longitudinal study. *Proceedings of the Royal Society B: Biological Sciences*, *280*,

719 20122231–20122231.

720 Weiss, A., Inoue-Murayama, M., Hong, K.-W., Inoue, E., Udono, T., Ochiai, T., Matsuzawa, T., Hirata, S., &

721 King, J. E. (2009). Assessing chimpanzee personality and subjective well-being in Japan. *American Journal*

722 *of Primatology*, *71*, 283-292.

723 Weiss, A., Inoue-Murayama, M., King, J. E., Adams, M. J., & Matsuzawa, T. (2012b). All too human?

724 Chimpanzee and orang-utan personalities are not anthropomorphic projections. *Animal Behaviour*, *83,* 1355-

725 1365.

726 Weiss, A., King, J. E., & Perkins, L. (2006). Personality and subjective well-being in orangutans (*Pongo*

727 *pygmaeus* and *Pongo abelii*). *Journal of Personality and Social Psychology, 90*, 501-511.

728 Weiss, A., King, J. E., & Hopkins, W. D. (2007). A cross-setting study of chimpanzee (*Pan troglodytes*)

729 personality structure and development: Zoological parks and Yerkes National Primate Research Center.

730 *American Journal of Primatology*, *69*, 1264-1277.

731 Weiss, A., Staes, N., Pereboom, J. J. M., Inoue-Murayama, M., Stevens, J. M. G., & Eens, M. (2015).

732 Personality in Bonobos. *Psychological Science, 26*, 1430-1439.

733 Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in*

734 *Ecology & Evolution, 27,* 1-10.

735 Yamamoto, M. E., Araujo, A., de Fatima Arruda, M., Lima, A. K. M., de Oliveira Siqueira, J., & Hattori, W. T.

736 (2014). Male and female breeding strategies in a cooperative primate. *Behavioural Processes*, *109*, 27-33.

737 Yamamoto, M.E., Domeniconi, C. & Box, H. (2004). Sex differences in common marmosets (*Callithrix*

738 *jacchus*) in response to an unfamiliar food task. *Primates, 45,* 249-254.

739

740 [1] Available at http://extras.springer.com/2011/978-1-4614-0175-9/weiss_monkey_personality.pdf

741

Table 1
Varimax-Rotated Component Loadings

Item	Con*	Agr	Ass*	Pat	Inq*	h^2
Thoughtless	**-0.81**	-0.15	-0.20	-0.07	-0.01	0.72
Bullying	**-0.80**	-0.32	0.16	-0.02	-0.04	0.78
Clumsy	**-0.80**	-0.08	-0.23	0.04	-0.26	0.77
Eccentric	**-0.79**	-0.14	-0.09	0.16	-0.15	0.71
Reckless	**-0.76**	-0.39	0.13	-0.07	0.12	0.77
Disorganized	**-0.72**	0.02	-0.11	-0.07	-0.22	0.59
Imitative	**-0.70**	-0.01	-0.27	-0.11	0.17	0.61
Erratic	**-0.69**	-0.28	-0.25	-0.01	-0.11	0.63
Jealous	**-0.69**	-0.36	0.14	0.13	0.08	0.64
Aggressive	**-0.68**	**-0.51**	-0.02	0.03	-0.05	0.74
Irritable	**-0.67**	**-0.56**	0.00	0.05	-0.05	0.77
Impulsive	**-0.66**	**-0.45**	0.09	-0.04	0.09	0.65
Excitable	**-0.63**	**-0.55**	-0.15	-0.03	-0.01	0.72
Unperceptive	**-0.61**	-0.09	0.00	-0.30	-0.24	0.53
Socially playful	**-0.58**	0.16	**-0.46**	0.10	0.34	0.71
Depressed	**-0.56**	-0.12	**-0.44**	0.21	**-0.43**	0.75
Stingy	**-0.53**	-0.32	0.30	0.02	0.05	0.48
Playful	**-0.51**	0.02	**-0.45**	0.21	**0.40**	0.67
Assertive	**-0.48**	-0.29	**0.46**	0.03	0.15	0.55
Friendly	0.20	**0.84**	-0.08	0.10	0.07	0.76
Equable	0.25	**0.74**	0.18	-0.01	-0.08	0.65
Affectionate	0.23	**0.73**	0.00	0.14	0.04	0.61
Permissive	**0.47**	**0.68**	0.03	-0.08	-0.10	0.70
Gentle	**0.56**	**0.67**	0.00	0.05	-0.06	0.76
Sociable	0.00	**0.63**	0.04	-0.12	0.36	0.54
Popular	0.10	**0.62**	**0.41**	-0.08	0.09	0.59
Helpful	0.14	**0.62**	-0.17	0.24	-0.12	0.50
Predictable	0.00	**0.55**	0.16	-0.09	-0.11	0.35
Unemotional	0.18	**0.54**	0.17	-0.20	-0.08	0.39
Protective	0.21	**0.50**	0.02	0.12	-0.13	0.32
Cautious	0.02	0.07	**-0.76**	-0.03	-0.31	0.68
Dependent	-0.15	-0.01	**-0.75**	-0.15	0.06	0.61
Dominant	-0.33	-0.06	**0.75**	-0.03	-0.03	0.67
Independent	-0.09	0.22	**0.73**	0.15	-0.07	0.62
Confident	0.08	0.24	**0.72**	0.15	0.28	0.69
Timid	-0.25	-0.31	**-0.71**	-0.08	-0.29	0.76
Submissive	-0.23	0.10	**-0.71**	0.10	-0.11	0.58
Fearful	-0.30	**-0.41**	**-0.68**	-0.08	-0.13	0.75
Tense	-0.26	**-0.44**	**-0.57**	-0.12	-0.27	0.67
Anxious	**-0.42**	-0.37	**-0.57**	0.03	-0.39	0.79

Vulnerable	**-0.56**	-0.21	**-0.56**	0.16	-0.31	0.79
Selective	-0.39	-0.03	**0.44**	0.17	-0.09	0.38
Sympathetic	0.09	0.35	**-0.43**	**0.40**	-0.23	0.52
Distractible	-0.22	0.05	-0.22	**-0.78**	0.02	0.71
Quitting	-0.26	0.08	-0.23	**-0.76**	-0.09	0.71
Intelligent	-0.07	0.01	0.02	**0.75**	0.22	0.62
Inventive	-0.23	-0.19	-0.23	**0.66**	0.27	0.65
Sensitive	-0.11	0.34	-0.14	**0.66**	-0.13	0.60
Persistent	**-0.40**	0.02	0.18	**0.65**	0.11	0.63
Patient	0.32	**0.47**	0.10	**0.50**	-0.04	0.59
Lazy	-0.16	0.36	-0.05	-0.02	**-0.68**	0.62
Exploratory	0.08	-0.01	0.18	0.38	**0.67**	0.64
Inquisitive	0.02	0.00	0.29	0.39	**0.65**	0.66
Active	-0.09	**-0.46**	-0.17	-0.10	**0.61**	0.63
Opportunistic	-0.25	-0.21	0.34	0.31	**0.53**	0.60
Solitary	-0.21	-0.25	-0.15	0.01	**-0.49**	0.36
Alert	0.05	0.00	0.33	-0.02	**0.43**	0.30
Proportion of variance	0.20	0.14	0.14	0.08	0.07	

Note. Con = Conscientiousness, Agr = Agreeableness, Ass = Assertiveness, Pat = Patience, Inq = Inquisitiveness, h^2 = communality. Bold typeface indicates loadings ≥ than |.4|.
*Loadings of this factor were reflected.

Table 2

The linear effects of sex and age on the component scores

			95% *CI*			
	b	*SE*	2.5%	97.5%	*t*	*p*
Conscientiousness						
Intercept	0.01	0.10	-0.19	0.21	0.14	.889
Sex	-0.01	0.10	-0.21	0.19	-0.07	.941
Age	-0.04	0.03	-0.11	0.02	-1.28	.204
Sex × Age	0.04	0.03	-0.03	0.11	1.21	.229
Agreeableness						
Intercept	0.02	0.10	-0.17	0.22	0.23	.817
Sex	0.11	0.10	-0.09	0.30	1.09	.277
Age	0.05	0.03	-0.02	0.11	1.49	.140
Sex × Age	**0.07**	**0.03**	**0.01**	**0.14**	**2.21**	**.029**
Assertiveness						
Intercept	0.01	0.10	-0.19	0.21	0.11	.909
Sex	-0.11	0.10	-0.31	0.09	-1.09	.277
Age	-0.03	0.03	-0.09	0.04	-0.76	.449
Sex × Age	0.03	0.03	-0.04	0.09	0.81	.421
Patience						
Intercept	0.03	0.09	-0.16	0.22	0.33	.740
Sex	**-0.30**	**0.09**	**-0.48**	**-0.11**	**-3.13**	**.002**
Age	-0.05	0.03	-0.11	0.01	-1.50	.136
Sex × Age	**0.07**	**0.03**	**0.01**	**0.14**	**2.36**	**.020**
Inquisitiveness						
Intercept	0.01	0.09	-0.18	0.19	0.06	.952
Sex	-0.15	0.09	-0.34	0.04	-1.59	.115
Age	**-0.13**	**0.03**	**-0.19**	**-0.07**	**-4.11**	**< .001**
Sex × Age	0.01	0.03	-0.05	0.07	0.25	.802